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RELATING RIPARIAN VEGETATION TO PRESENT AND FUTURE STREAMFLOWS[1]

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Abstract. The intense demand for river water in arid regions is resulting in widespread changes in riparian vegetation. We present a direct gradient method to predict the vegetation change resulting from a proposed upstream dam or diversion. Our method begins with the definition of vegetative cover types, based on a census of the existing vegetation in a set of 1 × 2 m plots. A hydraulic model determines the discharge necessary to inundate each plot. We use the hydrologic record, as defined by a flow duration curve, to determine the inundation duration for each plot. This allows us to position cover types along a gradient of inundation duration. A change in river management results in a new flow duration curve, which is used to redistribute the cover types among the plots. Changes in vegetation are expressed in terms of the area occupied by each cover type.

We applied this approach to riparian vegetation of the Black Canyon of the Gunnison National Monument along the Gunnison River in Colorado. We used TWINSPAN to cluster plots according to species occurrence. This analysis defined three vegetative cover types that were distinct in terms of inundation duration. Quantitative changes in the extent of cover types were estimated for three hypothetical flow regimes: two diversion alternatives with different minimum flows and a moving average modification of historical flows. Our results suggest that (1) it is possible to cause substantial changes in riparian vegetation without changing mean annual flow, and (2) riparian vegetation is especially sensitive to changes in minimum and maximum flows.

Principal advantages of this method are simplicity and reliance on relatively standard elements of plant community ecology and hydrologic engineering. Limitations include use of a single environmental gradient, restrictive assumptions about changes in channel geometry, representation of vegetation as quasi-equilibrium cover types, and the need for model validation.

Key words: bottomland vegetation; dam; discharge; diversion; environmental impact; flow duration; Gunnison; hydraulic model; riparian vegetation; TWINSPAN; vegetation change.

INTRODUCTION

Throughout the arid and semi-arid regions of western North America, riparian ecosystems are a conspicuous feature of the landscape. Riparian ecosystems are spatially and temporally dynamic and are shaped by fluvial as well as upland geomorphic processes. In spite of their limited areal extent in the West, these systems provide critical physical and biological linkages between terrestrial and aquatic environments (Gregory et al. 1991) and support many vertebrate species (Brinson et al. 1981).

Western riparian ecosystems have long been influenced by human activities; widespread modification began in the mid to late 1800s with diversion of streamflow primarily for irrigated agriculture (Wilkinson 1988, Knopf and Scott 1990). Subsequent trans-basin diversion projects and instream dams for water storage and flood control further altered riparian ecosystems (Johnson et al. 1976, Bradley and Smith 1986, Rood and Mahoney 1990). With increasing municipal, industrial, and recreational demands for western water and growing recognition of the resource values associated with riparian ecosystems (Lamb and Lord 1992), arid-region rivers will be subject to further conflicts, and managers will require quantitative predictions of ecosystem responses to altered stream discharge.

Several approaches have been used to relate stream discharge to riparian vegetation at individual sites. Stromberg and Patten (1990, 1991) used a site-specific regression between discharge and cottonwood growth to establish a flow standard for minimum flow. Bovee et al. (1978) and O'Keeffe and Davies (1991) estimated evapotranspiration from phreatophytic riparian vegetation in order to include this "consumptive use" of water in a multiple-use evaluation of streamflow. Stromberg (1993) related abundance of riparian vegetation to growing-season flow for a number of streams within a large watershed. Johnson (1992) developed a compartmental simulation model of changes in riparian cover types from water development along the Missouri River. Pearlstine et al. (1985) used an individual-based dynamic simulation to assess changes in woody riparian vegetation associated with hydrologic modi-

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fication in the Santee and Cooper river system in South Carolina. Species-specific establishment or maintenance criteria have also been used to explain patterns of riparian vegetation and to assess impacts of hydrologic alterations. For example, Rood and Mahoney (1990) explained the decline of western plains cottonwood forests downstream of dams by showing that the altered flows less frequently meet establishment requirements of cottonwood.

Franz and Bazzaz (1977) related the occurrence of riparian trees to inundation duration and then predicted how backwater from a proposed downstream reservoir would alter tree distribution. Harris et al. (1985) used hydraulic simulation models of the Instream Flow Incremental Methodology (Bovee 1982) to describe plant species distributions along belt transects orthogonal to the stream channel. We extend the approach of Franz and Bazzaz (1977), using hydraulic models similar to those of Harris et al. (1985), to predict the response of riparian vegetation to changes in discharge. Our method uses a direct gradient analysis to describe the present distribution of vegetation relative to inundation duration, as determined from a flow-duration curve for an appropriate period of record. A proposed dam or diversion has a predictable effect on the flow duration curve. We use the new flow duration curve in combination with our gradient analysis to predict the change in riparian vegetation for a reach of the Gunnison River in south-central Colorado.

Study Area

Black Canyon of the Gunnison National Monument is located along the Gunnison River on the western slope of the Rocky Mountains in Montrose County, Colorado, at longitude 107°45′ west and latitude 38°34′30″ north. The Monument was established in 1933 in recognition of the scenic quality of the steep-walled canyon cut into pre-Cambrian gneiss. In 1934 there was little vegetation in the canyon bottom (Warner and Walker 1972), probably because of the combined effects of alternating scouring floods and very low flows (Zimmerman 1969). Between 1936 and 1976, four dams were constructed on the Gunnison and Taylor rivers upstream of the Monument for power generation and irrigation (United States Department of the Interior 1990). Operation of the dams has reduced peak flows and raised low flows, allowing development of vegetation on the canyon bottom. This vegetation could be affected by future changes in water management.

The National Park Service chose a 450-m reach for intensive study. The width of the canyon bottom within this reach varies from 40 to 90 m, the gradient is 0.0128 m/m, and the elevation is ≈1707 m. The watershed area is 10 000 km² (Hansen 1987), and average annual precipitation is 370 mm (Colorado Climate Center 1984). Because of the steep canyon walls, the study reach is inaccessible to livestock and has probably never been grazed. Discharge is measured at East Portal, ≈14.5 river kilometres (distance along the river's path) upstream of the study reach at United States Geological Survey Gage 09128000 (Ugland et al. 1989). There are no dams, diversions, or important tributaries between the gage and the study reach. Because the closest dam upstream of the Monument is a reregulation dam, the Black Canyon is not subject to the large daily fluctuations in discharge associated with power-peaking operation of some hydroelectric dams. Peak discharge results from snowmelt and generally occurs in June (Fig. 1). The physicochemistry of this portion of the river is described by Stanford and Ward (1985). Ours is the first detailed description of the riparian vegetation of the Monument.

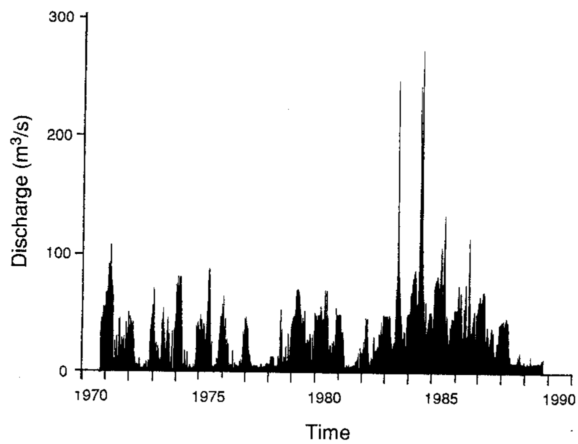

FIG. 1. Weekly average discharge of Gunnison River below Gunnison Tunnel.

Methods

Definitions

Five hydrologic terms are used frequently in this paper. *Discharge* is the flow of a stream in cubic metres per second. We used discharge data reported as daily averages. The *stage–discharge relation* is a curve relating discharge to the elevation of the water surface at a cross-section or point. The *flow regime* is the pattern of variation in discharge over time. *Flow duration* is the fraction of time a given discharge is equalled or exceeded. *Inundation duration* is the fraction of time a point on the bottomland is inundated. Flow duration and inundation duration are unitless quantities calculated using the hydrologic record for an appropriate period. The inundation duration of a point inundated once a year for a day is the same as that of a point inundated once every 7 yr for a week (0.00274).

Model overview

Our model is based on direct gradient analysis (Whittaker 1956, 1967, Bedinger 1979, Jongman et al. 1987), which describes the position of vegetation along environmental gradients. We related vegetation to the

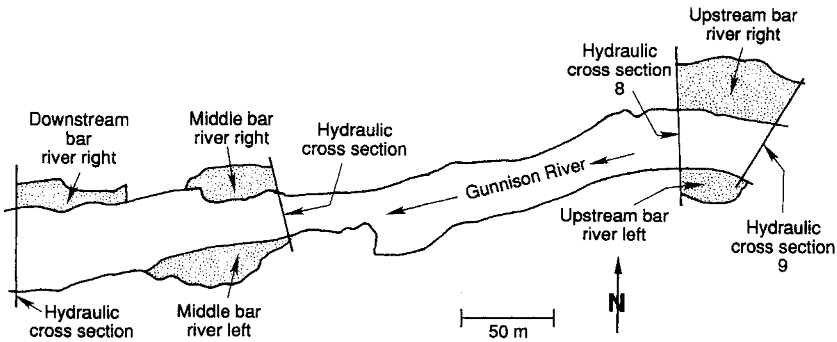

FIG. 2. Location of sampled areas within study reach.

gradient of inundation duration. Changes in vegetation distribution were then estimated by determining how a new flow regime would alter inundation durations. Franz and Bazzaz (1977) used a similar approach to assess the hydrologically simpler case of impoundment impacts upstream of a dam.

We censused randomly located plots, assigned each plot to one of three vegetative cover types, and determined the inundation duration for each plot based on the discharge required to inundate the plot and the historical flow duration curve. The inundation-duration gradient was broken into 12 regularly spaced classes. This number minimized the range of individual classes while ensuring that each class contained at least one plot. The 12 classes and the number of plots per class were: 0–0.01, 18 plots; 0.01–0.1, 42 plots; 0.1–0.2, 11 plots; 0.2–0.3, 3 plots; 0.3–0.4, 6 plots; 0.4–0.5, 10 plots; 0.5–0.6, 16 plots; 0.6–0.7, 16 plots; 0.7–0.8, 5 plots; 0.8–0.9, 5 plots; 0.9–0.99, 1 plot; 0.99–1.0, 0 plots. The 12th class in this list was not represented in the set of sampled plots, but was added in order to support prediction about plots that might become permanently inundated under an alternative hydrologic regime. For each class we calculated the proportion of plots in each cover type. We then used these proportions as probabilities to estimate the future cover type of a plot from its future inundation duration.

Flow duration curves describing different hydrologic alternatives were used to produce plot inundation durations associated with each alternative. Applying the cover-type probabilities to plots with new inundation durations produced an estimate of the expected value of the new number of plots in each cover type:

$$n_{i,j} = P_{i,j} \cdot T_j$$

where $n_{i,j}$ = number of plots in cover type i and inundation duration class j, $P_{i,j}$ = probability that a plot in inundation duration class j is in cover type i, T_j = total number of plots in inundation duration class j.

Application of the model to the plots sampled for calibration thus produces the expected number of plots in each cover type for each alternative hydrologic regime. We interpret changes in the proportions of randomly located plots as changes in the cover type composition of the study area. Ancillary model output includes fractions of time inundated and cover-type probabilities for each plot as well as transition matrices depicting aggregate and plot-by-plot change in inundation durations and cover-type probabilities.

We implemented the model as a series of individual modules, including the HEC-2 step-backwater model for water surface elevations (Hydrologic Engineering Center 1990), the TWINSPAN clustering program for identifying cover types (Hill 1979*a*), and a series of short programs that we wrote in FORTRAN and SAS (SAS Institute 1987) to interpolate water surface elevations, calculate flow duration curves, calibrate and apply cover-type probabilities, and summarize output across plots.

Plot sampling

We selected and sampled the plots on 18–31 July 1990. Vegetation sampling was restricted to the five relatively flat areas of alluvial sediment, or bars, within the study reach (Fig. 2). Adjacent to the stream, bars were delimited by the water's edge. This line also marked the streamward limit of emergent vegetation. Away from the stream, bars were bounded by the base of a cliff or the toe of a talus slope. The narrow, uneven areas of alluvial and colluvial sediment between bars were not sampled.

We randomly located 133 rectangular 1 × 2 m plots on the bars; the long side of each rectangle was placed parallel to the direction of flow. This plot size was big enough to represent the largely herbaceous vegetation and small enough that inundation duration was uniform throughout the plot. The center of each plot was located by reading x and y coordinates from a table of random numbers and pacing the coordinates in the field. The National Park Service prepared a topographic map of the study reach and determined the elevation and location of all the plots using a total station surveying instrument. The density of plots was intended to be the same for all bars; however, the total-station survey, carried out after the plots were established, indicated that plot densities on the five bars varied

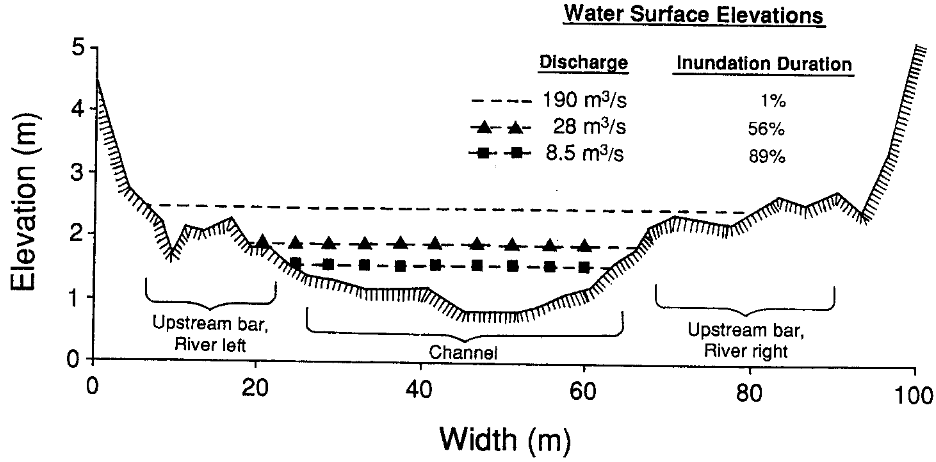

FIG. 3. Selected water surface elevations at cross section 8. Water elevations are those predicted from the hydraulic model; inundation durations of those discharges under the Reference hydrologic regime are also indicated. The location of this cross section is depicted in Fig. 2.

from 151 to 339 plots/ha. The total area of the five bars was 0.603 ha.

At each plot we determined the presence or absence of all vascular plant species using nomenclature following the United States Department of Agriculture (1982). We visually estimated total vegetative cover for each plot on a scale of 1 to 4: 1 = 0–25%; 2 = 26–50%; 3 = 51–75%, and 4 = 76–100%. Finally, we characterized the dominant substrate as organic matter, silt, sand, gravel, cobbles, or boulders. Two-way indicator species analysis (TWINSPAN) (Hill 1979*a*) was applied to the species occurrence data to cluster the plots into cover types. TWINSPAN was restricted to those 60 species that occurred in three or more plots. Detrended Correspondence Analysis (DCA, Hill 1979*b*) was applied to the same data set to illustrate the distribution of plots among cover types.

Hydrology

The model is based on the inundation duration of points in the riparian zone. First, the inundating discharge of a point was determined by comparing the surveyed elevation of the point to the stage–discharge relation. Then the inundation duration of the point was determined by comparing the inundating discharge to a flow duration curve.

Because the plots were scattered randomly across the bars and not confined to cross sections, it was necessary to construct a stage–discharge relation for each plot. The National Park Service established a series of nine hydraulic cross sections in the Monument, including four within the study reach (Fig. 2). The Park Service calibrated a hydraulic simulation model, HEC-2, (Hydrologic Engineering Center 1990, Hoggan 1989) to predict water surface elevations at the cross sections. The HEC-2 model was calibrated by five sets of field observations at discharges from 9.5 to 44.9 m^3/s and used to construct stage–discharge relations for each cross section. Fig. 3 illustrates calculated water surface elevations for several discharges at one of the hydraulic cross sections.

We used output from the water surface model to develop stage–discharge relations at each sampled plot for discharges of 0–283 m^3/s at increments of 0.6 m^3/s (20 cfs). For each discharge, the water surface elevations at cross sections upstream and downstream of a plot were read from the stage–discharge relations for these cross sections. The water surface elevation at a plot was then estimated by a linear interpolation based on the location of the plot along an idealized channel edge connecting the two cross sections.

Assuming a static channel geometry, the discharge necessary to inundate a point remains constant across different hydrologic regimes. However, each hydrologic regime has a different flow duration curve and thus produces a different inundation duration for a given point. The Reference hydrologic regime is the historical record of mean daily discharges from 1971 to 1989 obtained from a compilation of United States Geological Survey data (EarthInfo 1991). We describe results for three hydrologic alternatives: The Diversion alternative is a modification of the Reference regime in which each daily discharge is divided in half, except that discharge is not allowed to fall below 8.5 m^3/s (300 cfs). This minimum of 8.5 m^3/s has been voluntarily maintained by water managers since the early 1980s to protect the trout fishery of the Gunnison River (United States Department of the Interior 1990). In 1992, the Colorado Water Conservation Board obtained a senior water right of 8.5 m^3/s for instream flow maintenance; therefore, any future diversion would probably have to respect the 8.5 m^3/s minimum. The Diversion-Increased-Minimum alternative is identical to Diversion, except that the minimum flow is increased to 17.0 m^3/s. The Moving-Average alternative is a 1-yr moving average of the Reference regime. The

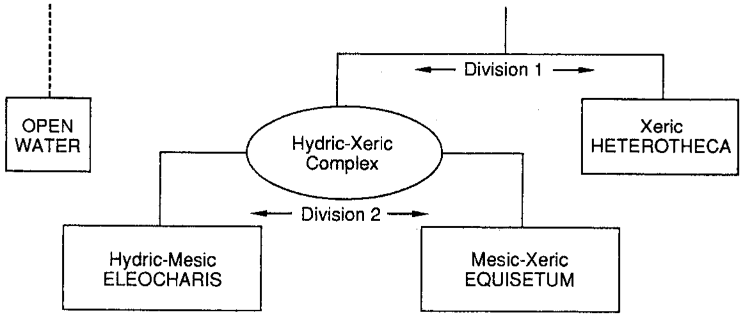

FIG. 4. Schematic of cover type classification.

Moving-Average alternative simulates the moderating effect that could be expected from additional upstream reservoir storage. Flow duration curves were constructed for each hydrologic regime by calculating the cumulative flow frequency distribution for the respective sets of daily discharge values.

RESULTS

Existing vegetation

Eighty-three vascular plant species were observed in the 133 plots. Vegetation was essentially herbaceous except for scattered, short (<2 m) individuals of *Acer negundo, Tamarix ramosissima,* and *Salix exigua* and a discontinuous fringe of mature *Acer negundo* and *Tamarix ramosissima* along the base of the canyon wall. Most of the plants recorded in the study reach are widely distributed species typical of low-elevation riparian zones in Colorado (Weber 1987, Kittel and Lederer 1993).

The first two divisions of TWINSPAN grouped the plots into three cover types (Fig. 4): Heterotheca, Equisetum, and Eleocharis. The distribution of plots among cover types is illustrated by the Detrended Correspondence Analysis ordination in Fig. 5. These cover

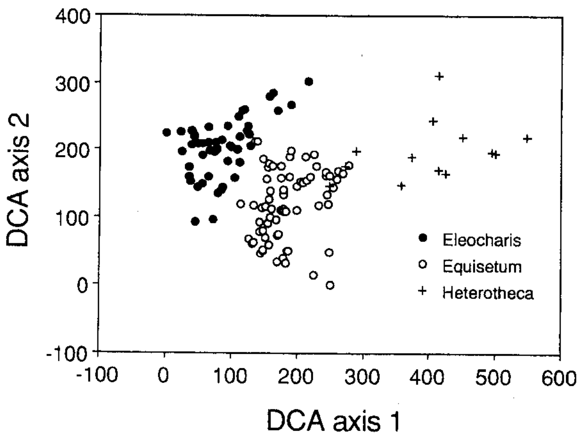

FIG. 5. Detrended Correspondence analysis (DCA) ordination of plots, by cover type, for the first two DCA axes. Eigenvalues for Axis 1 and Axis 2 were 0.56 and 0.27, respectively.

types, defined solely on the basis of species-occurrence data, occupied clearly different positions on the inundation-duration gradient (Fig. 6). In addition, a Kruskal-Wallis test (SAS Institute 1987) showed that the cover types were significantly different in inundation duration, vegetative cover, and soil particle size ($P < .0001$), demonstrating that floristic differences are strongly related to environmental gradients. A final cover type, Open Water, was added to account for the river channel and off-channel pools, which were unsampled areas, devoid of emergent vegetation, and inundated at the time of sampling. Based on stage-discharge information, this cover type was assigned an inundation duration of >99%.

The Heterotheca cover type consisted of xeric grasses and herbs dominated by *Bromus tectorum, Heterotheca villosa,* and *Sporobolus cryptandrus.* The plants most strongly associated with this cover type were largely upland species (Table 1, Reed 1988). Vegetative cover was sparse, usually 0–25%. The substrate was primarily sands, cobbles, and boulders. This cover type was confined to the upper portions of the Upstream, River Right bar (Fig. 2). This was the driest cover type (Fig. 6); its inundation duration was generally <2%.

The Equisetum cover type consisted of mesic to xeric herbs and grasses dominated by *Equisetum hyemale, Poa compressa, Agrostis stolonifera, Muhlenbergia racemosa,* and *Euthamia occidentalis.* Vegetative cover was mostly between 5 and 75%. The substrate was primarily organic matter and sands; however, some plots were dominated by boulders. This cover type was typically found on middle- and upper-elevation gravel and cobble bars. Generally, this was a relatively dry and infrequently inundated cover type (Fig. 6). Inundation durations ranged from ≈2 to 60%, with most plots in the range of 2–20%.

The Eleocharis cover type consisted of mesic herbs and grasses dominated by *Agrostis stolonifera, Euthamia occidentalis, Eleocharis palustris, Phalaris arundinacea, Poa palustris, Epilobium ciliatum,* and *Poa compressa.* Species with a high probability of occurring in wetlands (Reed 1988) were associated with this cover type (Table 1). Vegetative cover was highly variable, ranging from 25 to 100%. However, most

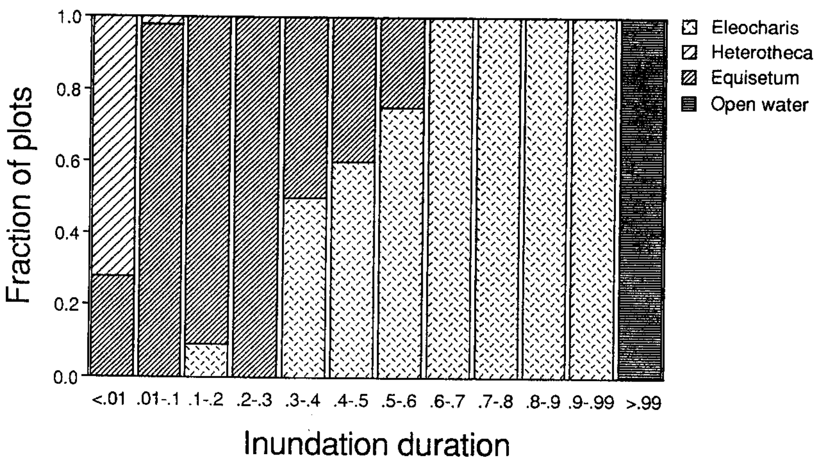

FIG. 6. Normalized distribution of cover types along gradient of inundation duration.

plots had from 50 to 75% cover. The substrate was also variable and consisted primarily of cobbles and boulders with large fractions of silt, sand, and organic matter. This was the wettest vegetated cover type and was found from the channel edge and the edge of off-channel pools, up to low and middle elevation gravel bars. This cover type was inundated frequently. Although the overall range of inundation duration was broad (Fig. 6), >80% of the plots had inundation durations between 50 and 89%. The low inundation durations calculated for some of the plots occupied by the Eleocharis cover type may reflect error in the hydraulic model, which does not consider the effects of sideslope drainage or localized depressions.

The Heterotheca cover type occurred on only 10.5% of the total bar area. Over half of the bar area (52.6%) was in the Equisetum cover type. The remaining 36.8% was occupied by the Eleocharis cover type. The Open-Water cover type did not occur in the set of sampled plots, but was defined based on the streamward limit of vegetation in order to support prediction about plots that might become permanently inundated under an alternative hydrologic regime.

Predicted vegetation changes

The flow duration curves for the Reference regime and the hydrologic alternatives are shown in Fig. 7. The Diversion alternative decreases mean flow to 54% of the Reference mean, and Diversion-Increased-Minimum decreases mean flow to 64%; the Moving-Average alternative involves no change in mean flow. All the alternatives decrease flow variability.

The model predictions of vegetation change under the alternative hydrologic regimes are shown in Table 2. Because the model is new and has not been field-tested, these predictions should be interpreted with caution. Equisetum remains the predominant cover type under all the alternatives (Table 2). Under the Diversion alternative some of the Eleocharis type is replaced by Equisetum. However, a larger area of Equisetum is converted to Heterotheca, and as a result the total area of Equisetum declines.

The Diversion-Increased-Minimum alternative increases mean flow by 19% relative to the Diversion alternative (Fig. 7); however, this additional water results in a decrease in the wettest vegetated cover type, Eleocharis (Table 2). The reason is that permanent inundation under the Diversion-Increased-Minimum alternative transforms some areas occupied by the Eleocharis cover type into Open Water.

The Moving-Average alternative decreases the area of the Equisetum and Eleocharis cover types and increases the area of both the driest cover type, Heterotheca, and the wettest type, Open Water (Table 2). As the extreme flow events are moderated, inundation duration increases where it was already high and decreases where it was already low. Thus a systematic reduction in the range of flow conditions toward the middle of the distribution actually increases the dispersion of cover types by increasing the area of cover types at the edges of the gradient.

DISCUSSION

Model utility

Our purpose in modeling vegetation dynamics is to incorporate a consideration of impacts on riparian vegetation into water management decisionmaking. In order to be practical the approach should be consistent with the conceptual, dimensional, and computational framework for making these decisions. Representing the river through a series of hydraulic cross-sections and modeling water surface elevations using Manning's equation or a step-backwater model are standard practices in water management. Likewise, summarizing hydrologic time series in flow duration curves is a common technique. Such curves would either be available as part of project engineering design or could be rea-

TABLE 1. Percentage of plots in each cover type containing selected species. Species with 10 or more total occurrences in the 133 plots are listed in order of their score on DCA (Detrended Correspondence Analysis) Axis 1. Wetland indicator status is from Reed (1988).

Species	Wetland indicator status*	Total occurrences	Cover type: Eleocharis	Cover type: Equisetum	Cover type: Heterotheca
			% occurrence		
Veronica anagallis-aquatica	OBL	11	22	0	0
Ranunculus cymbalaria	OBL	19	35	3	0
Epilobium ciliatum	FAC	30	59	1	0
Plantago major	FAC	27	51	3	0
Trifolium repens	FACU	21	39	3	0
Hordeum jubatum	FAC	10	18	1	0
Poa palustris	FACW	34	59	7	0
Eleocharis palustris	OBL	41	71	9	0
Melilotus alba	FACU	14	20	6	0
Mentha arvensis	FACW	12	12	9	0
Conyza canadensis	UPL	27	49	4	0
Phalaris arundinacea	OBL	51	71	23	0
Equisetum arvense	FAC	16	18	10	0
Acer negundo	FACW	38	55	14	7
Lactuca serriola	FACU	10	12	6	0
Euthamia occidentalis	OBL	99	96	75	0
Agrostis stolonifera	FACW	103	100	77	7
Agropyron sp.	...	22	6	28	0
Aster hesperius	OBL	12	0	17	0
Carex lanuginosa	OBL	57	35	57	7
Apocynum sp.	...	30	22	28	0
Cirsium arvense	FACU	24	16	23	0
Solidago sparsiflora	UPL	13	22	1	7
Verbena bracteata	FACU	16	22	6	7
Muhlenbergia racemosa	FACU	66	57	54	7
Juncus balticus	FACW	22	8	26	0
Verbascum thapsus	UPL	18	31	1	13
Carex nebrascensis	OBL	21	6	25	7
Poa compressa	FACU	97	63	90	27
Equisetum hyemale	FACW	75	18	91	20
Artemisia ludoviciana	FACU	46	55	22	27
Euphorbia serpyllifolia	UPL	10	10	6	7
Equisetum laevigatum	FACW	60	24	61	40
Chrysothamnus linifolius	UPL	10	18	0	7
Bromus tectorum	UPL	25	2	16	87
Heterotheca villosa	UPL	20	6	7	80
Sporobolus cryptandrus	FACU	14	0	4	73

* OBL = Obligate, >99% occurrence in wetlands; FACW = Facultative Wet, 67–99% occurrence in wetlands; FAC = Facultative, 34–66% occurrence in wetlands; FACU = Facultative Upland, 1–33% occurrence in wetlands; UPL = Upland, <1% occurrence in wetlands.

sonably requested from hydrologic engineers. Our direct-gradient prediction approach employs many of the same conceptual elements, computational procedures, and field methods as the Instream Flow Incremental Methodology (Bovee 1982, Harris et al. 1985), which is widely used to relate instream flow to fish habitat.

Relationships between vegetation and inundation duration could be formulated at either the species or cover-type level. Species tend to respond individualistically to environmental change, and this is the most appropriate level for understanding details of a temporally and spatially complex response. However, an overall synthesis is difficult when a large number of species are present. For this reason, we grouped the species into distinct cover types that become the basic units of vegetation description and change. The model could also be used to predict changes in abundance of individual species.

Finally, the basic output of the direct gradient model is a statement about the new, quasi-equilibrium vegetation associated with a new flow regime. This is a simplification of complex spatial and temporal response potentials. However, it has the strong advantage of being a single result, rather than a family of response curves. An alternative, the dynamic simulation model, naturally produces a family of output sequences in response to sequences of hydrologic input (e.g., Pearlstine et al. 1985). While these models are potentially more accurate and precise, their use dictates another complicated step to synthesize a family of possible vegetation responses. Vegetation response has to be represented simply enough to allow its inclusion as one of many variables (e.g., fish habitat, water supply, hydropower) considered in a water management decision. Furthermore, dynamic simulation models require more detailed autecological data than are available for many riparian species.

Inundation duration as the independent variable

Inundation duration, as determined by a flow duration curve, is the single environmental variable determining vegetation response in our model. The simplicity of this approach has both advantages and disadvantages. Many studies in humid regions (e.g., Wells 1928, Teversham and Slaymaker 1976, Teskey and Hinckley 1977, Bedinger 1979, Klimas et al. 1981, Harris et al. 1985, Hupp and Osterkamp 1985) have demonstrated that plant species and communities can be distinctly arrayed along a gradient of inundation duration. This study extends that conclusion to a semi-arid setting (Fig. 6), and we have obtained similar results in two as yet unpublished gradient analyses of riparian vegetation in the Colorado High Plains. Further studies are needed, particularly of herbaceous species, to determine whether our conclusions can be generalized to semi-arid and arid regions as a whole.

In many of the studies done in humid regions, inundation duration has been interpreted as a predictor of the degree of anoxia to which roots are exposed. However, in this western riparian application, inundation of most of the riparian zone is short-lived and anoxia is less important. Inundation duration succeeds here as a predictor of vegetation distribution because it is correlated with flow-related variation in a suite of environmental variables in the riparian zone. These include shear stress, sediment deposition and erosion, soil moisture, and depth to groundwater, in addition to soil oxygen concentration. For example, sites with a high inundation duration are likely to be closer to groundwater when not flooded, are likely to be inundated to greater depths when flooded, and are likely to be subject to greater and more frequent shear stress than sites with a low inundation duration.

Nonetheless, the relation of other environmental variables to inundation duration is imperfect. While the error involved in using a single surrogate measure may be acceptable for comparisons within a site, it does limit transferability of information between sites. For example, the position of a species on an inundation-duration gradient determined at a reach with groundwater recharge may be different from the position of the same species determined at a reach with groundwater discharge.

Although we judge inundation duration to be the best single independent variable for our purposes, no single variable can capture all the important aspects of water level change in a riparian area (Mitsch and Gosselink 1986). Alternative parameters may be superior in some situations. Both Hupp and Osterkamp (1985) and Bedinger (1979) arrayed riparian vegetation along a composite variable that combined inundation duration and recurrence interval. Recurrence interval can be defined as the average time between inundations for a particular point. The case of a bottomland downstream of a dam used for power peaking is an example of a situation suited for use of recurrence interval. In this case a point might be inundated for half of each day. It is essential to be able to distinguish such a point from another that is inundated continuously for 182 d and then dry for the next 182 d. Finally, the clear relationship between inundation duration and present vegetation (Table 1, Fig. 6) suggests, but does not prove, that anticipated changes in inundation duration can be successfully used to predict vegetation change. Verification of model predictions will be necessary to test the adequacy of our approach.

TABLE 2. Percentage of bar area occupied by each cover type under hydrologic alternatives.

Hydrologic alternative	Cover types: Open Water	Eleocharis	Equisetum	Heterotheca
Reference	0	37	53	10
Diversion	2	15	48	35
Diversion-Increased-Minimum	13	6	46	35
Moving-Average	2	33	37	28

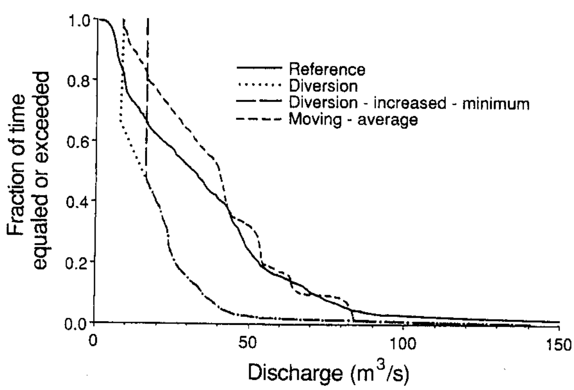

FIG. 7. Flow duration curves for hydrologic alternatives.

Channel change

Like most other methods used to predict changes in stream biota following flow alteration, the direct gradient method does not explicitly represent processes of channel change. This is not a problem if channel morphology is constant. However, if channel geometry changes, the calculated inundation durations of plots are likely to be in error. If bars move, but the areas of different surface types do not change, then the model predictions should still be valid. Where upstream dams are anticipated to cause major changes in channel width and depth (Williams and Wolman 1984) it will be necessary to predict their effect on the inundating discharges of a representative set of plots before using the direct gradient method to predict vegetation change.

Our study reach is a bedrock-controlled, steep-walled canyon cut into hard pre-Cambrian rock (Hansen 1987). The canyon walls preclude lateral migration or channel widening. The channel bed consists of cobbles and boulders over bedrock. The vegetated bars consist of cobbles and boulders sometimes covered by a layer of finer particles. The main sources of sediment to the Monument, both before and after dam construction, have been rock falls and debris flows within the canyon (Hansen 1987). Dam operation has moderated peak flows, preventing the stream from transporting the larger particles (Chase 1992). Therefore, the bed is relatively stable under current conditions and would remain so under the conditions of decreased peak flows addressed in the alternatives. A decrease in peak flows could result in channel narrowing by deposition of a new surface adjacent to the channel. However, such a surface would necessarily be small. Finally, under any of these alternatives a bar could be obliterated by a rock fall or debris flow, but these events will not be influenced by the alternatives under consideration.

Quasi-equilibrium vegetation

The direct gradient method assumes that the sampled vegetation and defined cover types are an adequate quasi-equilibrium expression of the longer term hydrologic regime. It does not require that the vegetation be constant, but it does require that variation over time does not obscure the relationship between vegetation and inundation duration. Conditions at the time of sampling on the Gunnison River were dry relative to the overall range of conditions in the 1971–1989 hydrologic record. Because calibration occurred during a period of low flow, the model tends to place cover types at incorrectly high inundation durations. The magnitude of the error depends on the flow conditions prior to the time in question. This source of error does not affect a relative analysis of alternatives like the current study. However, caution should be exercised when using the model to predict the precise vegetation composition at a specific time.

The predictions of our model have not yet been tested. The best way to validate the direct gradient method would be to repeat the plot sampling following a flow alteration. Sampling would have to be delayed long enough to allow the new flow regime to be expressed and to allow the vegetation to respond. The delay could be as short as 2 yr or as long as several decades, depending on the nature of the flow regime and the response time of the relevant vegetation. In the case of the three flow alterations considered here and their impacts on the largely herbaceous vegetation at our study site, a delay of roughly 10 yr might be necessary before validation could occur.

Implications for Management

The direct gradient method provides new, useful information about the effects of alternative flow regimes. Without the model, one might have predicted that diversion would cause a shift toward drier cover types, but the relative magnitude of the shift would have been unknown. More importantly, some of the predictions of the model are contrary to the conclusions a more cursory analysis might reach. A decrease in the variability of flow results in an increase in the relative abundance of the extreme cover types, and an increase in the minimum allowable flow results in a decrease in the area occupied by the wettest vegetated cover type.

Two general considerations are underscored by this analysis. First, it is possible to cause substantial changes in riparian vegetation without changing mean annual flow, as with the Moving-Average alternative. Second, special attention should be given to alternatives involving changes in flow boundaries. This includes both effectively implemented minimum flows and substantial reductions in peak flows. There are several reasons for being concerned about these hydrologic changes with respect to riparian vegetation. Changing the boundaries of the flow distribution creates new zones that are either always inundated or never inundated. Cover types in these zones (e.g., Open-Water) are generally the most structurally distinct from other cover types and exhibit little temporal fluctuation because of the constant conditions. In addition, establishment and mortality of riparian vegetation are episodic. Changing the boundary flows may eliminate the infrequent establishment opportunities in areas that are highly suitable for survival. Thus conflicts can arise between different goals of river management. The occasional high flows necessary for maintenance of some riparian plant species could damage property. The occasional low flows necessary for maintenance of other riparian species could decrease fish habitat. Models help make it possible to find a workable compromise.

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